

# Analysis of a Lagoon Ecological Model with Anoxic Crises and Impulsive Harvesting\*

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## Abstract

We analyze mathematically a system of impulsive nonlinear parabolic equations that model a shallow lagoon subject to anoxic crises and two types of impulsive harvesting. The main focus is on the existence and properties of periodic solutions. In particular we give conditions that ensure the existence of such solutions and examine the effect of harvesting on the occurrence of anoxic crises. Our approach is based on estimates on the principal eigenvalue of associated linear problems, and on results from Nonlinear Functional Analysis. In particular we obtain explicit criteria that involve the integrals of coefficients rather than maxima and minima. This is significant due to the large seasonal variations in the coefficient values.

*Index Terms*—lagoon ecology, anoxic crises, principal eigenvalue, impulsive systems.

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## 1 Introduction

It is the purpose of this paper to mathematically analyze the effects of biomass harvesting on an ecological model describing shallow lagoons ecological interactions. To be specific we

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consider a model based on ones proposed in papers by Ciaffi, Di Eugenio and Gallerano [1] and Ciaffi and Gallerano [2] — where more details (in particular values of coefficients) can be found — to describe the ecology in shallow lagoon of central Italy. These lagoons suffer from anoxic crises: under suitable conditions water layers with zero oxygen concentrations as well as high levels of hydrogen sulphide are present in the lagoon. Based on these models we consider a nonlinear coupled parabolic system involving four unknowns:  $S_1$  representing phytoplankton or floating microphytes concentrations;  $S_2$  representing rooted plants (*Ruppia* sp.) concentrations,  $O$  and  $H$  representing oxygen and hydrogen sulphide concentrations respectively. Since we must allow the possibility that oxygen may vanish in some layers, its equation is really an obstacle problem (with zero as the obstacle). Unlike the above references, we assume that nutrient levels are always very high and that all forms of carbon are proportional to the biomass densities  $S_1, S_2$ . These simplifications are given primarily for convenience of presentation, since the approach presented works in more general cases with obvious changes. It is well known that the interplay between water and bottom sediments is very important in determining the ecological behavior. We account for this by defining  $H(x, t)$  and  $O(x, t)$  for  $x$  in a domain  $\Omega$  that include both water and sediments, while the biomass is also defined for  $x$  in the whole  $\Omega$  not just the water, due to the assumption that carbon concentration is proportional to that of the biomass.

We introduce on this model two harvesting processes formally described below and roughly described as follows: in the first instance the biomass components, i.e.  $\int_{\Omega} S_i(x, t) dx$ , for  $i = 1, 2$ , are measured at a given time  $t_2$  each year. If they exceed a threshold value  $a_i$  then biomass is removed until it is reduced to  $a_i$  at a specified later time  $t_1$ . In the second approach, harvesting is started at a given time  $t_2$  (regardless of the biomass levels) and reduced to a specified fraction  $\alpha_i(x)$  at time  $t_1$ . As we show below, it suffices to treat the cases where the two times are  $t_1^-$  and  $t_1^+$ , i.e. with the harvesting viewed as an impulsive phenomenon, since the other cases can be reduced to this one.

We establish in particular conditions for the existence of positive periodic solutions for the two harvesting processes, and show that if the harvesting effort is increased then in one harvesting procedure we still have positive periodic biomass (albeit small), but this is impossible for the other harvesting procedure. Furthermore we show that if there is “sufficient” harvesting in one procedure, then  $O$  is always positive so that no anoxic layers forms. We also give sufficient conditions on the coefficients for crises to occur regularly.

Our analysis is based primarily on a suitable reduction of impulsive periodic problems to related non-impulsive problems, and a detailed examination of the principal periodic eigenvalue. It is important for us to obtain estimates on the eigenvalues which depend on coefficient averages rather than pointwise estimates. For this we draw on results from [9]. Our existence process is topological and this approach is most important in the situation of the first harvesting process which leads to non-local terms in the equations. It is in part based on a perturbation that guarantees that solutions stay above any bifurcation.

Our paper outline is as follows. In Section 2 we introduce the model and basic assumptions. In Section 3 we consider a linear impulsive periodic problem and show how this can

be reduced to a non-impulsive case. This reduction may introduce jumps in the coefficients. We thus find it convenient to work with  $C^{\alpha, \alpha/2}$  spaces. In Section 4 we obtain conditions based on suitable eigenvalues estimates for the existence of positive periodic solutions via topological methods. In Section 5 we examine the consequences of the two harvesting procedures. In Section 6 we obtain some explicit sufficient conditions on the coefficients to ensure that the eigenvalue estimates of Section 4 hold. Finally Section 7 gives conditions for crises to occur.

In conclusion we observe that there is a vast literature on these topics. For the readers interested in lagoon ecological model development and simulations, besides the above references [1], [2] we also mention the book [3] and papers [4], [5], [6], [7], [8], [9], [16], [17], where many other references may be found. But as far as the mathematical analysis of these ecological models is concerned we are only aware of the two papers [4], [9]. The mathematical analysis of periodic eigenvalue problems and/or impulsive problems is also vast. For the non-impulsive eigenvalue problem we recall the classic book by Hess, [10], where the subject is developed. For impulsive problems applied to biological questions there is also a long history ([13]) and a recent reference is [12]. There are also numerous papers on general impulse questions: [11], [14], [15]. Harvesting processes have also been considered, see e.g.: [18], [19]. Finally in [20] a non-local problem with application to biology is discussed.

The interested reader will find many other references in the cited papers. While the above references have some relation to what we discuss, with the closest earlier work probably being [9], we were not able to find the problem we present here discussed mathematically elsewhere.

## 2 The model

The earlier considerations lead to the following ecological model:

$$\begin{aligned}
(1) \quad \ell_1(S_1) &\triangleq \frac{\partial S_1}{\partial t} - \nabla[D_{S_1} \nabla S_1 + \vec{b}_{S_1} S_1] \\
&= [N_{S_1,1}(x, t) - N_{S_1,2}(x, t, O, H)S_1 - N_{S_1,3}(x, t)S_2]S_1 \triangleq F_1(S_1, S_2, O, H)S_1 \\
(2) \quad \ell_2(S_2) &\triangleq \frac{\partial S_2}{\partial t} - \nabla[D_{S_2} \nabla S_2 + \vec{b}_{S_2} S_2] \\
&= [N_{S_2,1}(x, t) - N_{S_2,2}(x, t)S_1 - N_{S_2,3}(x, t, O, H)S_2]S_2 \triangleq F_2(S_1, S_2, O, H)S_2 \\
(3) \quad \ell_H(H) &\triangleq \frac{\partial H}{\partial t} - \nabla[D_H \nabla H + \vec{b}_H H] \\
&= -N_{H,1}(x, t)OH + N_{H,2}(x, t, O)(S_1 + S_2) \triangleq F_H(S_1, S_2, O, H) \\
(4) \quad \ell_O(O) &\triangleq \frac{\partial O}{\partial t} - \nabla[D_O \nabla O + \vec{b}_O O] \\
&= [N_{O,1}(x, t)S_1 + N_{O,2}(x, t)S_2] - [N_{O,3}(x, t)S_1 + N_{O,4}(x, t)S_2]\chi(O) \\
&\quad - N_{O,5}(x, t)OH \\
&\triangleq F_O(S_1, S_2, O, H)
\end{aligned}$$

In these equations all coefficient functions are assumed positive (except for the drift coefficients  $\vec{b}_{S_1}, \vec{b}_{S_2}, \vec{b}_H, \vec{b}_O$ ), smooth except for the characteristic function  $\chi$  — albeit very different in the water as compared to the sediments — and bounded in their respective arguments. The functions  $N_{S_1,2}, N_{S_2,3}$  are taken to be monotone non-increasing (respectively: non-decreasing) with respect to  $O$  (resp.:  $H$ ), while  $N_{H,2}$  is assumed to be non-increasing in  $O$ . Note that this is not a standard competitive system. We recall that (1), (2), (3), (4) hold in  $\Omega$  (water and sediments). With equations (1)–(2) we associate natural (no flux) homogeneous boundary conditions, i.e.

$$D_{S_i} \frac{\partial S_i}{\partial n} + \vec{b}_{S_i} \cdot \vec{n} S_i = 0 \quad \text{for } i = 1, 2 \text{ on } \partial\Omega,$$

while for (3) and (4) we assume on  $\partial\Omega$ :

$$(5) \quad D_0 \frac{\partial O}{\partial n} + \vec{b}_O \cdot \vec{n} O + a_1 O = a_2$$

$$(6) \quad D_H \frac{\partial H}{\partial n} + \vec{b}_H \cdot \vec{n} H + b_1 H = 0$$

with  $a_1, a_2, b_1$  non-negative non-trivial smooth functions.

We comment briefly on the significance of the coefficient functions, and direct the interested reader to our references [1], [2] where a much more detailed explanation is given. The left hand side of equations (1)–(4) involve the usual diffusion (turbulent and molecular) and drift (water currents) processes. The right hand side of equations (1)–(2) are of the classical Lotka-Volterra competitive type. They take into account the effect of the exogenous inputs (light, wind, temperature, nutrients), as well as the effects of oxygen and hydrogen sulphide. The right hand side of (3) has terms representing aerobic re-oxidation and anaerobic production. The right hand side of (4) accounts for the effects of photosynthesis, of consumption due to respiration and to re-oxidation. Finally the right hand side of (5) describes the interchange with the oxygen in the atmosphere.

Observe that equation (4) is viewed as a classical obstacle problem (with zero as the obstacle) thus ensuring that the oxygen levels remain non-negative at all times. This is achieved by replacing the characteristic function

$$\chi(\xi) = \begin{cases} 1 & \xi > 0 \\ 0 & \xi \leq 0 \end{cases}$$

on the right side of (4) by a family of functions  $\chi_n(\xi)$  with  $\chi_n(\xi)$  smooth, monotone and:  $\chi_n(\xi) = 0$  if  $\xi \leq \frac{1}{n}$ ;  $\chi_n(\xi) = 1$  if  $\xi \geq \frac{2}{n}$ . Henceforth we assume that this has been done, and obtain below the final result for the original system (1)–(4) by passing to the limit as  $n \rightarrow \infty$  and employing the Banach-Sachs Theorem. Finally, we consider a situation where in an attempt to control the onset of possible crises, some of the biomass is harvested yearly

— over a very short period — at given times  $t_n$ , chosen for simplicity to occur at the same time each year. This process is assumed to occur based upon measurements of the biomass components at an earlier time  $t_n^*$  of the year. Specifically we assume for  $i = 1, 2$  that

$$(7) \quad S_i(x, t_n^+) = g_i \left( \int_{\Omega} S_i(x, t_n^{*-}) dx \right) S_i(x, t_n^{*-})$$

with

$$g_i(\xi) = \begin{cases} 1 & \xi \leq a_i \\ a_i/\xi & \xi > a_i \end{cases}$$

where  $a_i > 0$  represent chosen threshold values. We observe that employing  $t_n^+$ ,  $t_n^{*-}$  allows the possibility that  $t_n^* = t_n$ , i.e. that the harvest is an impulsive effect. System (1)–(4) is now to hold for all  $t \neq t_n$ , while at  $t = t_n$  condition (7) is applied. Observe that condition (7) implies that the biomass of  $S_i$  at  $t_n^+$  does not exceed  $a_i$ : it is reduced to this value if the biomass at  $t_n^*$  exceed  $a_i$ , otherwise no harvest take place.

Clearly related to (7) is the harvesting process:

$$(8) \quad S_i(x, t_n^+) = \alpha_i(x) S_i(x, t_n^{*-})$$

with  $0 < \alpha_i \leq 1$ . In this situation, the harvesting occurs regardless of the biomass quantity at  $t_n^*$ . For process (8) we show that for any given  $N_{S_i,1}$ , if  $\alpha_i$  is chosen small enough, then we have  $S_i \rightarrow 0$  as  $t \rightarrow \infty$ .

There are two possible problems: the periodic situation and the initial value problem. We focus here on the former case. The situation in the latter case can be considered in the same way with obvious changes to the approach we explicitly present. We thus consider equations (1)–(4) with the given boundary conditions, harvesting process (7) or (8) and seek a periodic solution for the interval  $0 \leq t \leq T$ . All coefficients/data are assumed periodic in time with this period. The harvesting process described by (7) or (8) is assumed to take place at a time  $t_1$  with observation at time  $t_2$  with  $0 < t_2 < t_1 < T$  and then periodically repeated with period  $T$ . We seek conditions for the existence of a periodic solution, with  $S_1, S_2, H, O$  non-negative non-trivial. As may be expected, the investigations involve the properties of a distinguished eigenvalue of impulsive periodic-parabolic problems, which we first consider for convenience in a prototype situation.

### 3 Problem reduction and parabolic eigenvalues

Let  $Q_T = \Omega \times (0, T)$  and  $t_1 \in (0, T)$ . Consider the impulsive parabolic operator formally given by:

$$(9) \quad \ell(w) = w_t - \nabla[a \nabla w + \vec{b} w] + cw$$

in  $Q_T$ , for  $t \neq t_1$ , with coefficients in  $C^\infty$ , except we allow  $c$  to have simple jump discontinuities at specified times, and  $a > \delta > 0$  for some constant  $\delta$ . With  $\ell$  are associated: natural boundary conditions on  $\partial\Omega$ ; periodicity conditions:  $w(x, 0) = w(x, T)$ ; the impulsive condition  $w(x, t_1^+) = \beta w(x, t_1^-)$  with  $\beta > 0$  constant. We indicate at the end of the section the changes needed to treat the cases where  $\beta = \beta(x)$  and/or  $t_1^-$  is replaced by  $t_2$  with  $0 < t_2 < t_1$ .

We first reduce the problem to a “standard” case by incorporating the impulsive condition in the expression for  $\ell$  as follows: define  $A(t)$  by

$$(10) \quad A(t) = 1 + H_f(t - t_1)[\beta^{-1} - 1]$$

where  $H_f(\xi)$  denotes the Heaviside unit step function, and let  $h(t)$  be a positive smooth function such that  $A(0)h(0) = A(T)h(T) = 1$ . For example we may choose  $h$  to be a mollified  $A^{-1}$ . Observe that  $A'(t) = 0$  if  $t \neq t_1$ . Suppose now  $f \in L^p(Q_T)$  for  $p$  suitably large. Then results in [21] show that if  $w$  solves the non-impulsive periodic problem

$$(11) \quad \ell(w) - \frac{h'}{h}w = fhA$$

with  $h' = \frac{dh}{dt}$ , we must have  $w \in C^{\alpha, \alpha/2}(\overline{Q}_T)$  for some  $\alpha > 0$ . Now setting  $u = w/(hA)$  gives directly that  $u$  is periodic and satisfies  $\ell(u) = f$  if  $t \neq t_1$ , while at  $t = t_1$  we have:

$$u(t_1^+) = \frac{w(t_1^+)}{h(t_1^+)A(t_1^+)} = \frac{w(t_1^-)\beta}{h(t_1^-)A(t_1^-)} = u(t_1^-)\beta.$$

Thus the impulsive condition is satisfied. We may consider henceforth the impulsive problems associated with (9) in terms of the non-impulsive problem (11).

We can thus state the following result which extends the one given in [9] (which is based in part on classical results of [22]) to the present impulsive case. Set  $\tilde{C}_A^{\alpha, \alpha/2}(\overline{Q}_T) = \{u : Au \in C^{\alpha, \alpha/2}(\overline{Q}_T)\}$ . We emphasize that  $\alpha$  denotes a generic constant,  $0 < \alpha < 1$ , which may change within the same proof or from proof to proof.

**Theorem 1** *The following statements hold:*

- (a) *The impulsive periodic parabolic eigenvalue problem  $\ell(w) = \mu w$  has a unique principal real eigenvalue  $\mu$  with corresponding positive eigenvector  $w \in \tilde{C}_A^{\alpha, \alpha/2}(\overline{Q}_T)$ .*
- (b)  *$\mu$  is continuous with respect to  $c$  (in the  $L^p$  norm for  $p$  sufficiently large) and  $\beta$ . It is monotone with respect to  $c$ .*
- (c) *The impulsive periodic problem  $\ell u = f \in \tilde{C}_A^{\alpha, \alpha/2}(\overline{Q}_T)$  has a non-negative solution  $u \in \tilde{C}_A^{\alpha, \alpha/2}(\overline{Q}_T)$  for any  $f \geq 0$  iff  $\mu > 0$ .*

$$(d) \quad \mu \leq \inf_{\phi \in H^1(\Omega)} \int_{\Omega} \left[ \tilde{a} |\nabla \phi|^2 + (\tilde{\vec{b}} \cdot \nabla \phi) \phi + \left( \tilde{c} + \left[ \frac{|\tilde{\vec{b}}|^2}{4a} \right] - \frac{\ln \beta}{T} \right) \phi^2 \right] dx$$

where  $\tilde{r} \triangleq \frac{1}{T} \int_0^T r dt$ . Let  $\delta(t)$  satisfy for  $t \in [0, T]$

$$\delta(t) \leq \inf \left\{ \int_{\Omega} [(a(x, t) \nabla \phi + \vec{b}(x, t) \phi) \cdot \nabla \phi + c(x, t) \phi^2] dx : \phi \in H^1(\Omega), \|\phi\|_{H^1} = 1 \right\}.$$

$$\text{Then } \mu \geq \frac{1}{T} \int_0^T \delta(t) dt - \frac{\ln \beta}{T}.$$

(e) Let  $u \geq 0$ ,  $u \in \tilde{C}_{A, \text{loc}}^{\alpha, \alpha/2}[\overline{\Omega} \times (0, +\infty))$ , solve the impulsive initial value inequality  $\ell u \leq 0$  with  $u(x, 0) = u_0(x)$  and homogeneous natural boundary conditions. We assume that the coefficients and the impulsive times are periodic. If  $\mu > 0$  then  $u(\cdot, t) \rightarrow 0$  in  $L^\infty(\Omega)$  as  $t \rightarrow \infty$ .

**Proof.** Observe that  $\mu$  is the principal eigenvalue to the non-impulsive problem:

$$\ell(z) - \frac{h'}{h} z = \mu z$$

iff  $\mu$  is the principal eigenvalue of the impulsive problem  $\ell(w) = \mu w$  with  $w = z/hA$ . Proofs of parts (a), (b), (c), (d) follow immediately from the non-impulsive results given in [9] which also hold in the case of  $c$  with jumps. In particular, for part (d), observe that  $\int_0^T h'/h dt = \ln \beta$ , while the lower estimate for  $\mu$  comes from choosing  $\phi = z$ .

Finally, for part (e), observe that  $w = hAu$  solves the non-impulsive inequality

$$\ell(w) - \frac{h'}{h} w \leq 0$$

with  $h$  and  $A$  continued by periodicity. The non-impulsive periodic problem also has eigenvalue  $\mu > 0$  and so does its adjoint  $\ell^*$ , i.e.

$$\ell^*(z) - \frac{h'}{h} z = \mu z$$

with  $z$  periodic and  $\mu > 0$ . We thus obtain, for any chosen  $t = t_0 > 0$ ,

$$\mu \int_{t_0}^{t_0+nT} \int_{\Omega} zw = \int_{t_0}^{t_0+nT} \int_{\Omega} \left[ \ell^*(z) - \frac{h'}{h} z \right] w = - \int_{\Omega} zw \Big|_{t_0}^{t_0+nT} + \int_{t_0}^{t_0+nT} \int_{\Omega} z \left[ \ell(w) - \frac{h'}{h} w \right]$$

i.e.

$$(12) \quad \int_{\Omega} zw \Big|_{t_0+nT} + \mu \int_{t_0}^{t_0+nT} \int_{\Omega} zw \leq \int_{\Omega} zw \Big|_{t_0}.$$

Since  $z$  is positive, bounded above and below, by periodicity we conclude for any  $\epsilon > 0$ , by the choice  $t_0 = 0$  and  $n$  large, that there exists  $\tilde{t}$  with  $\int_{\Omega} w|_{\tilde{t}} < \epsilon$ . Whence, by choosing  $t_0 = \tilde{t}$  in (12) we obtain that  $\int_{\tilde{t}}^{\infty} \int_{\Omega} w < K\epsilon$ . We now apply the results of [23] to conclude  $\|w(\cdot, t)\|_{L^{\infty}(\Omega)} \rightarrow 0$  as  $t \rightarrow \infty$ . The result follows.  $\blacksquare$

We conclude this section with the following observations.

**Remark 1** If  $\beta = \beta(x)$ , then the same approach can be used, but now terms involving  $\nabla_x \beta$ ,  $\nabla_x A$  arise in the equivalent non-impulsive problem. Specifically the impulsive equation  $\ell(u) = f$  is reduced to the non-impulsive problem

$$(13) \quad w_t - \frac{h'}{h} w - hA \nabla \left[ a \nabla \left( \frac{w}{hA} \right) + \vec{b} \frac{w}{hA} \right] = hA f$$

with  $A = A(x, t)$  still given by (10) but with now

$$\beta = \beta(x), \quad h(x, 0)A(x, 0) = h(x, T)A(x, T) = 1 \quad \text{and} \quad h' \triangleq \frac{\partial h}{\partial t}.$$

A variant of Theorem 1 is immediately applicable to (13), but the expressions (particularly of the analogue of the estimate in Part (d)) are more complicated.

**Remark 2** Suppose that  $t_1^-$  is replaced by  $t_2$  (with  $t_2 < t_1$ ) in the impulsive condition:  $u(t_1^+) = \beta u(t_2)$ . This corresponds to the harvesting process occurring for  $t \in (t_2, t_1)$  and reducing the biomass by a factor of  $\beta$ . This problem can be treated in the same way by a time shift for  $t \geq t_1^+$  in the coefficients as follows: consider the periodic impulsive problem

$$(14) \quad \begin{cases} v_t - \nabla [\hat{a} \nabla v + \vec{\hat{b}} v] + \hat{c} v = \hat{f} \\ v(t_2^+) = \beta v(t_2^-) \end{cases}$$

with:

$$\hat{a}(x, t) = \begin{cases} a(x, t) & 0 \leq t \leq t_2 \\ a(x, t + \Delta t) & t_2 < t \leq T - \Delta t \end{cases}$$

$\Delta t = t_1 - t_2$ ,  $T$  replaced by  $T - \Delta t$ . An identical shift for  $t \geq t_1^+$  is done to obtain  $\hat{b}$ ,  $\hat{c}$ ,  $\hat{f}$ . We treat problem (14) by the above methods, and find the solution  $v$ . We then obtain  $u$  by:

$$u(x, t) = \begin{cases} v(x, t) & 0 \leq t \leq t_2 \\ z(x, t) & t_2 < t \leq t_1 \\ v(x, t + \Delta t) & t_1 < t \leq T \end{cases}$$

where  $z(x, t)$  solves the initial value problem  $\ell z = f$ ,  $z(x, t_2) = v(x, t_2)$ . Observe that the values of the coefficients  $a$ ,  $\vec{b}$ ,  $c$  in the interval  $(t_1, t_2)$  are not significant in determining the properties of the principal periodic parabolic eigenvalue. However the “period” has been reduced to  $T - \Delta t$  from  $T$  in the estimates. If  $T - \Delta t$  is sufficiently small, then the “impulsive” term  $\frac{\ln \beta}{T - \Delta t}$  in Theorem 1 becomes dominant for  $\beta \neq 1$ .



## 4 The existence of a positive periodic impulsive solution

We seek conditions for a periodic solution to system (1)–(4) under one of the harvesting processes (7), (8) where — for simplicity of presentation — we choose:  $\alpha(x)$  equal to a constant in (8),  $t_n^* = t_1$  in (7) and  $\chi(O)$  replaced by a smooth function  $\chi_n(O)$  in (4). The more general situation can be considered by the procedures outlined above.

We incorporate the harvesting effects on  $S_1$ ,  $S_2$  into system (1)–(4) by the process of Section 3. Specifically, we replace (1)–(4) by

$$(15) \quad \ell_1(S_1^*) - \frac{h'_1}{h_1} S_1^* = F_1 \left( \frac{S_1^*}{h_1 A_1}, \frac{S_2^*}{h_2 A_2}, O, H \right) S_1^*$$

$$(16) \quad \ell_2(S_2^*) - \frac{h'_2}{h_2} S_2^* = F_2 \left( \frac{S_1^*}{h_1 A_1}, \frac{S_2^*}{h_2 A_2}, O, H \right) S_2^*$$

$$(17) \quad \ell_H(H) = F_H \left( \frac{S_1^*}{h_1 A_1}, \frac{S_2^*}{h_2 A_2}, O, H \right)$$

$$(18) \quad \ell_O(O) = F_O \left( \frac{S_1^*}{h_1 A_1}, \frac{S_2^*}{h_2 A_2}, O, H \right).$$

As discussed above, a solution of the impulsive system (1)–(4) can be obtained from a solution of the non-impulsive system (15)–(18) by setting  $S_1 \triangleq S_1^*/(h_1 A_1)$ ,  $S_2 \triangleq S_2^*/(h_2 A_2)$ . Note that for the harvesting process (7) we have  $\beta_i = g_i \left[ \int_{\Omega} S_i(s, t_1^-) \right]$  and thus

$$A_i(t) = 1 + H_f(t - t_1) \left[ \left( g_i \left[ \int_{\Omega} S_i(x, t_1^-) \right] \right)^{-1} - 1 \right].$$

Observe that  $A_i(t_1^-) = 1$ , and now for convenience we choose  $h_i(t)$  such that  $h_i(t_1^-) = 1$  also. Thus

$$\int_{\Omega} \frac{S_i^*}{h_i A_i} \Big|_{t_1^-} = \int_{\Omega} S_i^* \Big|_{t_1^-}.$$

It is also convenient to note that for both (7) and (8) we have  $h'/h \leq 0$  by construction.

We consider first harvesting process (8) (with  $\alpha_i(x) = \alpha_i$  constant). For this it is convenient to consider first the following sub-problems. Let  $\hat{S}_1^* \geq 0$ ,  $\hat{S}_2^* \geq 0$  denote the solutions of the decoupled equations for  $S_1^*$ ,  $S_2^*$  for the “best” ecological case for  $S_1^*$ ,  $S_2^*$ :

$$(19) \quad \ell_1(\hat{S}_1^*) - \frac{h'_1}{h_1} \hat{S}_1^* = \left[ N_{S_1,1} - \inf_{\xi, \tau \geq 0} \{ N_{S_1,2}(x, t, \xi, \tau) \} \frac{\hat{S}_1^*}{h_1 A_1} \right] \hat{S}_1^*$$

$$(20) \quad \ell_2(\hat{S}_2^*) - \frac{h'_2}{h_2} \hat{S}_2^* = \left[ N_{S_2,1} - \inf_{\xi, \tau \geq 0} \{ N_{S_2,3}(x, t, \xi, \tau) \} \frac{\hat{S}_2^*}{h_2 A_2} \right] \hat{S}_2^*.$$

We allow the possibility that (one of)  $\widehat{S}_1^*, \widehat{S}_2^* = 0$ . Consider then the decoupled principal eigenvalue problem:

$$(21) \quad \ell_1(w_1) - \frac{h'_1}{h_1} w_1 - \left[ N_{S_1,1} - \frac{N_{S_1,3} \widehat{S}_2^*}{h_2 A_2} \right] w_1 = \mu_1 w_1$$

$$(22) \quad \ell_2(w_2) - \frac{h'_2}{h_2} w_2 - \left[ N_{S_2,1} - \frac{N_{S_2,2} \widehat{S}_1^*}{h_1 A_1} \right] w_2 = \mu_2 w_2 .$$

we then have:

**Theorem 2** *Let harvesting process (8) hold and assume the eigenvalues  $\mu_1, \mu_2$  of (21), (22) respectively are negative. Suppose the elliptic parts of  $\ell_H, \ell_O$  are coercive. Then system (15)–(18) has a solution  $(S_1^*, S_2^*, H, O)$  with  $S_1^*, S_2^*, H, O$  positive in  $\Omega$  and  $S_1^*, S_2^*, H, O \in C^{\alpha, \alpha/2}(\overline{\Omega} \times [0, T])$ .*

**Proof.** Rewrite system (15)–(18) in the form  $\vec{\mathcal{L}}[\vec{G}] = \vec{F}(\vec{G})$  with:  $\vec{\mathcal{L}} = \text{diag}(\ell_1 + k, \ell_2 + k, \ell_3, \ell_4)$ ;  $\vec{G} = (S_1^*, S_2^*, H, O)^T$ ;  $\vec{F}(\vec{G}) = ((\frac{h'_1}{h_1} + k + F_1)(S_1^*)^+, (\frac{h'_2}{h_2} + k + F_2)(S_2^*)^+, F_H, F_O)^T$ , for some chosen large  $k$ . Let  $0 < \epsilon < 1$  be chosen and consider the approximate problem  $\vec{\mathcal{L}}[\vec{G}] = \vec{F}(\vec{G}) + \epsilon(1, 1, 0, 0)^T \triangleq \vec{Z}(\vec{G})$ . We write  $\vec{G} \in C^{\alpha, \alpha/2}$  if  $S_1^*, S_2^*, H, O \in C^{\alpha, \alpha/2}(\overline{\Omega} \times [0, T])$ . If now  $0 \leq \lambda \leq 1$  is also chosen, then we have that the problem  $\vec{\mathcal{L}}[\vec{G}] = \lambda \vec{Z}(\vec{G})$  (with  $\lambda$  also multiplying the non-homogenous part of the boundary conditions) cannot have solution  $\vec{G}$  on  $\|\vec{G}\|_{C^{\alpha, \alpha/2}} = R$  for some  $\alpha$  and some  $R$  independent of  $\epsilon$ . This is immediate for  $S_1^*, S_2^*$  by the positivity of  $N_{S_1,3}, N_{S_2,2}$ . These then bound  $H, O$ . Furthermore the map  $(\vec{\mathcal{L}})^{-1}[\vec{Z}(\vec{G})]$  is continuous and completely continuous from  $C^{\alpha, \alpha/2}$  to itself by classic results in [21], [23]. We then have the existence of a positive  $C^{\alpha, \alpha/2}$  solution to the perturbed system. We now let  $\epsilon \rightarrow 0$  and observe that the resulting sequence of  $S_1^*$  is bounded in  $C^{\alpha, \alpha/2}$  and cannot go to zero. Indeed, if  $S_1^* \rightarrow 0$  as  $\epsilon \rightarrow 0$ , then  $S_2^* \not\rightarrow 0$  due to (21) and, in the limit,  $S_2^*$  must be no greater than  $\widehat{S}_2^*$  of (20) by simple subtraction. But this contradicts the assumption that the principal eigenvalue  $\mu_1$  of (21) is negative by Theorem 1(c). By exactly the same argument,  $S_2^* \not\rightarrow 0$  in  $C^{\alpha, \alpha/2}$ , whence also  $H, O \not\rightarrow 0$  in  $C^{\alpha, \alpha/2}$ . We conclude the existence of a positive solution.  $\blacksquare$

We now pass to a consideration of harvesting process (7). In this case  $h_i$  depends on  $\int_{\Omega} S_i^*|_{t_1^-}$ , and we note that now  $A_i = h_i = 1$  at  $t_1^-$  by choice of  $h_i$ . Furthermore equations (19)–(20) will still have a positive solution  $\widehat{S}_1^*, \widehat{S}_2^*$  if the least eigenvalues  $\delta_i$  of  $\ell_i(w_i) - N_{S_i,1} w_i = \delta_i w_i$  are negative as  $h'_i \leq 0$  and  $h'_i \equiv 0$  if  $\widehat{S}_i^*$  is small enough.

Conditions under which  $\widehat{S}_1^*, \widehat{S}_2^*$  are unique are now not clear due to the presence of the nonlocal term  $\int_{\Omega} \widehat{S}_i^*$  in  $h_i$  for  $i = 1, 2$ .

**Theorem 3** *Let the harvesting process (7) hold and assume that the terms  $h'_i/h_i$  have been dropped from the left hand side of equations (21)–(22). If the principal eigenvalues  $\mu_1, \mu_2$  of (21)–(22) are negative for any solutions  $\hat{S}_1^*, \hat{S}_2^*$  of (19)–(20) and the elliptic parts of  $\ell_H, \ell_O$  are coercive, then the conclusion of Theorem 2 holds.*

**Proof.** The procedure is similar to that of Theorem 2, except for the fact that  $h_i$  depends continuously on  $\int_{\Omega} S_i^*|_{t-}$ . Observe however that  $h'_i$  is still non-positive, whence the boundedness of  $S_1^*, S_2^*$  for the perturbed problems follows by noting that  $h_1 A_1 = 1$  except for  $t$  in some small interval. On the other hand, integration and periodicity imply

$$\max_t \int_{\Omega} (S_1^*)^2 \leq K \min_t \int_{\Omega} (S_1^*)^2$$

for some constant  $K$ , whence

$$\int_{Q_T} N_{S_1,1} (S_1^*)^2 \leq K_1 \int_{Q_T \cap \{h_1 A_1 = 1\}} (S_1^*)^2$$

for some constant  $K_1$ . It follows that  $S_1^*$  is bounded in  $L^2$  and thus in  $L^\infty$  and finally in  $C^{\alpha, \alpha/2}$ .

Finally observe that if  $S_1^* \rightarrow 0$  then  $h'_1 = 0$  for  $S_1^*$  small enough (specifically:  $S_1^* < a_1$ ) and  $S_2^* \not\rightarrow 0$  by (21). In the limit,  $S_2^*$  must be no smaller than  $\hat{S}_2^*$  (a solution of (20)). Once again this contradicts (21) (with  $h'_1/h_1 = 0$ ). The rest of the proof is identical.  $\blacksquare$

We cannot conclude from Theorems 2 and 3 that in the limit as  $\chi_n \rightarrow \chi$  we maintain  $O$  strictly positive in  $\Omega$ . Indeed  $O$  vanishing in parts of  $\Omega$  is possible, as we consider in Section 7. Note that the conditions on the elliptic parts of  $\ell_H, \ell_O$  will hold if  $\vec{b}_H, \vec{b}_O$  are small due to conditions (5)–(6) by estimates similar to those of Theorem 1(d).

## 5 Consequence of harvesting and non-existence of periodic solutions

In Section 4, results were obtained that relate the existence of positive solutions to the existence and properties of the solutions of the decoupled equations (19)–(22). Note in particular that, if  $N_{S_1,1}, N_{S_2,1}$  are sufficiently high (so that (21)–(22), with  $h'_i/h_i$  set  $\equiv 0$ , have negative eigenvalues), then the harvesting problem (7) will allow the existence of positive periodic solutions regardless of the size of the positive thresholds  $a_i$ . This seems intuitively reasonable, since harvesting does not take place if the biomass of  $S_i$  does not exceed  $a_i$ . Observe however that with this process  $\int_{\Omega} S_i|_{t+} \leq a_i$ . Since  $0 \leq S_i$  satisfies  $\ell_i(S_i) \leq N_{S_i,1} S_i$ , in view of the boundary conditions we conclude

$$\frac{d}{dt} \left[ \int_{\Omega} S_i \right] \leq \|N_{S_i,1}\|_{L^\infty} \left[ \int_{\Omega} S_i \right]$$

i.e.  $\int_{\Omega} S_i|_t \leq Ca_i$  by periodicity, for some  $C = C(\|N_{S_{i,1}}\|, T)$ . In the same way, chose a value  $t^* \neq t_1$ , put  $\widehat{S}_i = \widehat{S}_i^*/(h_i A_i)$  in (19)–(20) and thus, since  $\widehat{S}_i$  solves the periodic impulsive system corresponding to (19)–(20) with  $\int_{\Omega} \widehat{S}_i|_{t_1} \leq a_i$ , we obtain  $\int_{\Omega} \widehat{S}_i|_t \leq K_i a_i$  for some constant  $K_i$ . Observe that for  $t$  near  $t^*$ ,  $\widehat{S}_i$  is a classical solution of the impulsive problem, and we have  $\|\widehat{S}_i(\cdot, t^*)\|_{L^\infty} \leq K'_i a_i$  for some  $K'_i$ . Then for  $t \geq t^*$ ,  $\widehat{S}_i$  cannot exceed the solution  $z_i$  of the linear problem:

$$\ell_i(z_i) - N_{S_{i,1}}(z_i) = 0 \quad z_i|_{t=t^*} = K'_i a_i .$$

We conclude again by periodicity that  $\widehat{S}_i = \widehat{S}_i^*/(h_i A_i) \leq K''_i a_i$  for some  $K''_i$  independent of  $a_i$ . Inserting this estimate in (21)–(22) and recalling that  $h'_i/h_i$  can be disregarded we obtain that (21)–(22) have negative eigenvalues for  $a_i$  small enough (by the non-triviality of  $N_{S_{i,1}}, N_{S_{i+1,1}}$ ) if the drifts are also small. Thus if the harvesting is intense enough while the drift terms are small, then the (periodic) biomass is kept small and furthermore so is  $\|H\|_{C^{\alpha, \alpha/2}(\overline{Q}_T)}$ , i.e. the levels of hydrogen sulphide, while due to the non-homogeneous boundary conditions for oxygen — accounting for the interchange with the atmosphere — we conclude from (4) that, if  $a_i$  are small enough, the oxygen levels are always positive (equivalently  $O$  is above the obstacle) and no anoxic layer develops. This is further discussed in Section 7.

The situation is somewhat different with harvesting process (8). Indeed, if  $\alpha_i$  is small enough, then for a given set of coefficients we have by Theorem 1(d) that  $\mu_i > 0$ . This coupled with  $\ell_i(S_i) - N_{S_{i,1}} S_i \leq 0$  shows that  $S_i \rightarrow 0$  by Theorem 1(c). That is: if the harvesting level is high enough — as estimated by the positivity of the principal eigenvalue — then no positive periodic solution are possible for the biomass.

## 6 Eigenvalue estimates

We focus on obtaining sufficient conditions for the existence of a positive periodic solution for the harvesting process (8), i.e. the existence of a positive solution to (19) and of a corresponding negative eigenvalue to (22), (the situation for the pair (20)–(21) is identical), with  $A_i, h_i$  as given by (10) with  $\beta = \alpha_i$ . Observe that for the existence of a unique positive  $\widehat{S}_1^*$  it suffices that the least eigenvalue  $\delta_1$  of

$$\ell_1(w_1) - \left[ N_{S_{1,1}} + \frac{h'_1}{h_1} \right] w_1 = \delta_1 w_1$$

be negative. The choice  $\phi \equiv 1$  in Theorem 1(d) shows that for this it suffices that:

$$(23) \quad \frac{1}{|\Omega|} \int_{Q_T} N_{S_{1,1}} dx dt > -\ln \alpha_1 + \frac{1}{|\Omega|} \int_{Q_T} \frac{|\vec{b}_{S_1}|^2}{4D_{S_1}} dx dt.$$

Assuming that (23) holds then  $\widehat{S}_1^*$  exists and we require (again by the choice  $\phi \equiv 1$  in Theorem 1(d))

$$(24) \quad \frac{1}{|\Omega|} \int_{Q_T} \left[ N_{S_2,1} - \frac{N_{S_2,2}}{h_1 A_1} \widehat{S}_1^* \right] dxdt > -\ln \alpha_2 + \frac{1}{|\Omega|} \int_{Q_T} \frac{|\vec{b}_{S_2}|^2}{4D_{S_2}} dxdt.$$

On the other hand, we have by periodicity

$$(25) \quad \int_{Q_T} N_{S_1,1} \widehat{S}_1^* = \int_{Q_T} \frac{F(\widehat{S}_1^*)^2}{h_1 A_1} - \int_{Q_T} \frac{h'_1}{h_1} \widehat{S}_1^*$$

with  $F \triangleq \inf_{\xi, \eta > 0} N_{S_1,2}(x, t, \xi, \eta)$ . Equation (25) implies by the positivity of  $-h'_1$  that

$$(26) \quad \int_{Q_T} \frac{F(\widehat{S}_1^*)^2}{h_1 A_1} \leq \int_{Q_T} \frac{h_1 A_1 N_{S_1,1}^2}{F}.$$

Consequently,

$$(27) \quad \int_{Q_T} \frac{N_{S_2,2}}{h_1 A_1} \widehat{S}_1^* \leq \left( \int_{Q_T} \frac{N_{S_2,2}^2}{h_1 A_1 F} \right)^{1/2} \left( \int_{Q_T} \frac{h_1 A_1 N_{S_1,1}^2}{F} \right)^{1/2}.$$

It follows that (24) holds if

$$(28) \quad \int_{Q_T} N_{S_2,1} > -\ln \alpha_2 + \frac{1}{|\Omega|} \left( \int_{Q_T} \frac{N_{S_2,2}^2}{h_1 A_1 F} \right)^{1/2} \left( \int_{Q_T} \frac{h_1 A_1 N_{S_1,1}^2}{F} \right)^{1/2} + \frac{1}{|\Omega|} \int_{Q_T} \frac{|\vec{b}_{S_2}|^2}{4D_{S_2}} dxdt.$$

In summary, if the harvesting parameters  $\alpha_i$  in the process (8) and the equation coefficients satisfy conditions (23) and (28), then system (1)–(4) has a positive periodic impulsive solution.

## 7 The occurrence of crises

We conclude by obtaining some simple explicit conditions on the coefficient integrals that ensure that anoxic crises will occur regularly. This is equivalent to showing that system (1)–(4) — with  $\chi(O)$  replaced by unity — cannot have classical solutions with  $O$  strictly positive. Equivalently, system (1)–(4) must have for any solution the oxygen levels actually equal to zero in some subregions of  $Q_T = \Omega \times [0, T)$  of positive measure. The calculations are in part similar to those of Section 6, and we present them for simplicity only in the case of vanishing cross-terms:  $N_{S_1,3} = N_{S_2,2} \equiv 0$  and no harvesting nor drift terms. The same

approach can be used in the general case, but the calculations are longer and the result more complicated. Put, for convenience:

$$\begin{aligned}\overline{N}_{1,2} &= \sup_{\xi, \tau \geq 0} N_{S_1,2}(x, t, \xi, \tau), \\ \overline{N}_{2,3} &= \sup_{\xi, \tau \geq 0} N_{S_2,3}(x, t, \xi, \tau), \\ \underline{N}_{1,2} &= \inf_{\xi, \tau \geq 0} N_{S_1,2}(x, t, \xi, \tau), \\ \underline{N}_{2,3} &= \inf_{\xi, \tau \geq 0} N_{S_2,3}(x, t, \xi, \tau).\end{aligned}$$

We then have

**Theorem 4** *Assume no harvesting, no drift and  $N_{S_1,3} = N_{S_2,2} = 0$ . If:*

$$\begin{aligned}& \frac{\left(\int_{Q_T} N_{S_1,1}^{3/4}\right)^4}{|Q_T| \left(\int_{Q_T} \frac{N_{S_1,1}^2}{\overline{N}_{1,2}}\right) \left(\int_{Q_T} \frac{\overline{N}_{1,2}^2}{N_{O,3}}\right)} + \frac{\left(\int_{Q_T} N_{S_2,1}^{3/4}\right)^4}{|Q_T| \left(\int_{Q_T} \frac{N_{S_2,1}^2}{\overline{N}_{2,3}}\right) \left(\int_{Q_T} \frac{\overline{N}_{2,3}^2}{N_{O,4}}\right)} \\ & \geq \int_0^T \int_{\partial\Omega} a_2 + \left(\int_{Q_T} \frac{N_{O,1}^2}{\underline{N}_{1,2}}\right)^{1/2} \left(\int_{Q_T} \frac{N_{S_1,1}^2}{\underline{N}_{1,2}}\right)^{1/2} + \left(\int_{Q_T} \frac{N_{O,2}^2}{\underline{N}_{2,3}}\right)^{1/2} \left(\int_{Q_T} \frac{N_{S_2,1}^2}{\underline{N}_{2,3}}\right)^{1/2},\end{aligned}$$

then system (1)–(4) cannot have classical solutions with  $O$  positive.

**Proof.** We note that  $S_1$  (resp.:  $S_2$ ) must satisfy  $S_1 \geq \widehat{S}_1^*$  (resp.:  $S_2 \geq \widehat{S}_2^*$ ) with  $\widehat{S}_1^*$  (resp.:  $\widehat{S}_2^*$ ) solution of (19) (resp.: (20)), with  $h'_i \equiv 0$  and inf replaced by sup. Observe that (19) then implies by multiplication by  $(\widehat{S}_1^*)^\alpha$ , for suitable  $\alpha$ , integration and periodicity:

$$\begin{aligned}\int_{Q_T} N_{S_1,1} (\widehat{S}_1^*)^{-1/2} &\leq \int_{Q_T} \overline{N}_{1,2} (\widehat{S}_1^*)^{1/2}, \\ \int_{Q_T} N_{S_1,1} \widehat{S}_1^* &= \int_{Q_T} \overline{N}_{1,2} (\widehat{S}_1^*)^2, \\ \int_{Q_T} N_{S_1,1} &\leq \int_{Q_T} \overline{N}_{1,2} \widehat{S}_1^*,\end{aligned}$$

whence

$$\int_{Q_T} \overline{N}_{1,2} (\widehat{S}_1^*)^2 = \int_{Q_T} N_{S_1,1} \widehat{S}_1^* \leq \left(\int_{Q_T} \frac{N_{S_1,1}^2}{\overline{N}_{1,2}}\right)^{1/2} \left(\int_{Q_T} \overline{N}_{1,2} (\widehat{S}_1^*)^2\right)^{1/2},$$

i.e.:

$$\int_{Q_T} N_{S_1,1} \widehat{S}_1^* \leq \int_{Q_T} \frac{N_{S_1,1}^2}{\overline{N}_{1,2}}.$$

We then obtain

$$\begin{aligned} \int_{Q_T} N_{S_1,1}^{3/4} &= \int_{Q_T} \frac{N_{S_1,1}^{1/2}}{(\widehat{S}_1^*)^{1/4}} (\widehat{S}_1^*)^{1/4} N_{S_1,1}^{1/4} \\ &\leq \left( \int_{Q_T} \frac{N_{S_1,1}}{(\widehat{S}_1^*)^{1/2}} \right)^{1/2} \left( \int_{Q_T} \widehat{S}_1^* N_{S_1,1} \right)^{1/4} |Q_T|^{1/4} \\ &\leq \left( \int_{Q_T} \frac{N_{S_1,1}}{(\widehat{S}_1^*)^{1/2}} \right)^{1/2} \left( \int_{Q_T} \frac{N_{S_1,1}^2}{\overline{N}_{1,2}} \right)^{1/4} |Q_T|^{1/4}, \end{aligned}$$

that is:

$$\frac{\left( \int_{Q_T} N_{S_1,1}^{3/4} \right)^2}{\left( |Q_T| \int_{Q_T} \frac{N_{S_1,1}^2}{\overline{N}_{1,2}} \right)^{1/2}} \leq \int_{Q_T} \frac{N_{S_1,1}}{(\widehat{S}_1^*)^{1/2}} \leq \int_{Q_T} \overline{N}_{1,2} (\widehat{S}_1^*)^{1/2} \leq \left( \int_{Q_T} \frac{\overline{N}_{1,2}^2}{N_{O,3}} \right)^{1/2} \left( \int_{Q_T} N_{O,3} \widehat{S}_1^* \right)^{1/2},$$

with  $N_{O,3}$  the term occurring in equation (4). We conclude:

$$(29) \quad \int_{Q_T} N_{O,3} S_1 \geq \int_{Q_T} N_{O,3} \widehat{S}_1^* \geq \frac{\left( \int_{Q_T} N_{S_1,1}^{3/4} \right)^4}{|Q_T| \left( \int_{Q_T} \frac{N_{S_1,1}^2}{\overline{N}_{1,2}} \right) \left( \int_{Q_T} \frac{\overline{N}_{1,2}^2}{N_{O,3}} \right)}.$$

In exactly the same way, we obtain:

$$(30) \quad \int_{Q_T} N_{O,4} S_4 \geq \frac{\left( \int_{Q_T} N_{S_2,1}^{3/4} \right)^4}{|Q_T| \left( \int_{Q_T} \frac{N_{S_2,1}^2}{\overline{N}_{2,3}} \right) \left( \int_{Q_T} \frac{\overline{N}_{2,3}^2}{N_{O,4}} \right)}.$$

We also have by integrating equation (19) and replacing  $N_{S_1,2}$  by  $\underline{N}_{1,2}$

$$\int_{Q_T} \underline{N}_{1,2} S_1^2 \leq \left( \int_{Q_T} \frac{N_{S_1,1}^2}{\underline{N}_{1,2}} \right)^{1/2} \left( \int_{Q_T} \underline{N}_{1,2} S_1^2 \right)^{1/2}.$$

Thus

$$(31) \quad \int_{Q_T} N_{O,1} S_1 \leq \left( \int_{Q_T} \frac{N_{O,1}^2}{N_{1,2}} \right)^{1/2} \left( \int_{Q_T} \frac{N_{S_1,1}^2}{N_{1,2}} \right)^{1/2}$$

and in the same way,

$$(32) \quad \int_{Q_T} N_{O,2} S_2 \leq \left( \int_{Q_T} \frac{N_{O,2}^2}{N_{2,3}} \right)^{1/2} \left( \int_{Q_T} \frac{N_{S_2,1}^2}{N_{2,3}} \right)^{1/2}$$

Finally, integrating equation (4) gives in this case:

$$(33) \quad \int_0^T \int_{\partial\Omega} a_1 O = \int_0^T \int_{\partial\Omega} a_2 - \int_{Q_T} N_{O,5} O H + \int_{Q_T} [N_{O,1} S_1 + N_{O,2} S_2] - \int_{Q_T} [N_{O,3} S_1 + N_{O,3} S_2].$$

Replacing the last two terms by the estimates (29)–(32) and noting that  $H \geq 0$  cannot vanish identically due to the positivity of  $S_1 + S_2$ , implies  $\int_0^T \int_{\partial\Omega} a_1 O + \int_{Q_T} N_{O,5} O H < 0$ . We conclude that  $O$  must be negative somewhere, and thus all solutions of (1)–(4) must have  $O$  equal to zero in some sub-domains of  $Q_T$ . ■

Observe that while the condition of Theorem 4 is complicated, heuristically it states that respiration ( $N_{O,1}$ ,  $N_{O,2}$ ) must be dominant. The effect of harvesting is, intuitively, to lower  $N_{S_1,1}$ ,  $N_{S_2,1}$ . If these coefficients are small enough then the condition of Theorem 4 is not valid, due to the term  $\int_0^T \int_{\partial\Omega} a_2$ . This is in keeping with the expectation that crises will not take place if enough harvesting is done. Finally, the result of Theorem 4 and those of Section 6 do not take particular advantage of the structure of the left hand side of system (1)–(4). We expect that the onset of crises will also be aided by a drop in the oxygen diffusivity in parts of the lagoon. Some results can possibly be obtained in such a case by replacing the test functions chosen in the above arguments by functions whose support is essentially in the part of the lagoon of interest.

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